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Is Otolith Growth Representative of Cohort Growth?

by

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ABSTRACT.-

The growth rates of different Flemish Cap Cod cohorts are compared for the period 1980 to 1991. Back-calculation of fish lengths based on their otqliths is used to study cod growth in this area. Growth turns out to be linear until the age of 8 years, after which there is a marked decline.

This method did not reveal significant growth differences between cohorts; but mean length at age data obtained from research cruise samples do show growth differences between cohorts, and the 1985 and 1986 cohorts stand out for their low growth rates.

It is suggested that growth variations in the fish are not necessarily reflected in otolith growth, so that growth differences between cohorts cannot necessarily be detected from back-calculation of fish lengths based on their otoliths.

INTRODUCTION.-

Flemish Cap (NAFO Div. 3M) is an isolated bank of the North American Continental Shelf. It is separated from the Grand Bank by Flemish Pass with depths greater than 1000 m, which presumibly impedes migrations of the more important species, among them the cod, between Flemish Cap and the Newfoundland Banks.

Flemish Cap cod is an ideal population to study variations in year class strength, and the interactions between fishing, environment and the life history strategy (Akenhead 1982).

This cod stock is relatively large, genetically isolated, and shows great fluctuations in abundance (Lear 1981, Templeman 1976).

From the environmental point of view, this stock occurs in a small area with special and well-known oceanografic features at the boundary zone between the cold Labrador Current and the warmer and more saline North Atlantic Current. This situation can cause sharp gradients in oceanografic conditions (Keeley 1982).

The growth of Flemish Cap cod has been studied before (Bishop 1977, Wells 1983). Here we compare the growth by cohorts obtained by back-calculation from the otoliths with estimates of growth based on research cruise samples in the area.

It is well known that cod growth rates vary geographically and also interannually within the same area. In Flemish Cap, these variations have been decribed by Bishop (1977) and Wells (1983 b). The relation between the biological parameters of the stock considered here and environmental conditions have not been clearly shown.

P-Gandaras and Zamarro (1990) established relations between growth, abundance and age at first maturity of each cohort, and proposed that these relations are established early at critical times for each cohort. They suggested that the differing conditions in which the juveniles developed, such as cohort abundance, water temperature and food availability, produced changes in the linear growth rates of flemish Cap cod during their first years of life.

Since it is difficult to obtain directly mean length at age data to study the growth of different cohorts, we decided to back calculate these lengths, and to compare the growth differences seen by each cohort by the two methods.

MATERIAL AND METHODS.-

For this study, 4785 otoliths obtained from samples taken on commercial vessels since 1987 were used, as well as from research cruises to Flemish Cap in 1988, 1989, 1990 and 1991. In the 1990 cruise, as well as demersal trawls, various shots with pelagic gear were made, and 15 cod of age group 0 were captured in the pelagic phase.

For each fish, length, weight and sex were recorded together with the data and depth of capture.

One otolith was used for age determination, done by two readers, and in the case of disagreement by a third. After this they were arranged by cohort, and within each cohort by age and sex. The otoliths in best conditions were selected so that for each cohort a maximum of 100 were available covering all lengths, and for as many depths and seasons as possible (Table I).

Otoliths were cleaned by agitation in vials in distilled water at 30ºC for 12 hours. They were then dried in an oven at 60ºC for 24 hours, and weighed on a Metler H80 balance with 0.1 mg precision.

Otolith lengths (LOTO), were measured with a Mitutoyo electronic caliper to 0.01 mm precision, and data recorded automatically. Data were stored in a VAX 4200 computer and processed using BMDP statistical programmes (Dixon et al 1990).

The high correlation found between the ages read and the lengths or weights of the otoliths led to a selection, based on analysis of the residuals, of those otoliths suitable for further study. Thus for each age and cohort, those otoliths were chosen as good in which the residuals of the age were less than 0.1; or as possibly in error by one year more (residuals less -0.9) or one year less (residuals greater than 1). A further otolith sample was taken radomly from each age group and cohort. These were used to differentiate the different kinds of otoliths which can exist, as well as to detect possible errors in reading.

In this way 713 otoliths were selected. These were embedded in polyester resin and 0.8 mm sections cut which included the nuclei. These sections were examined with a binocular microscope in transmitted ligth to identify structures characteristic of the cohorts, and to measure the rings.

Rings were measured using a camera lucida (magnification = X35) attached to the binocular and the Mitutoyo electronic caliper. Measurements were made from the nucleus to the beginning of the next opaque zone. Thus the first year includes the nucleus and the first winter ring. Successive years were measured from the beginning of one opaque zone to the beginning of the next. When possible, all measurements were made along an axis crossing the nucleus and cutting the edge of the otolith in the internal external direction (fig. 1).

Errors derived from difficulties in locating the nucleus and others derived from faulty sections were rectified by multiplying the measurements by a factor which simultaneously relate the diameter and length of otolith. This variable was used due to its high correlation with fish length, and because its error is less relative to otolith measurements.

Thus:

$$ANi = \frac{LOTO/10}{AA'} D(i) \qquad (1)$$

D(i) = Distance to ring (i).
AA' = Diameter of otolith.

Both D(i) and AA' are derived from the camera lucida images. Otolith length (LOTO) is divided by 10 so that this procedure gives results close to the real ones.

Recent summaries and critiques of the back-calculation technique (Gutreuter 1987, Francis 1990, Campana 1990) have been reviewed.

On the basis of the different hypotheses and techniques in use, and the critical revisions of these methods, we have developed the following procedure, in which our data acquisition (see equation 1) makes it more convenient to use otolith length as the variable used in the regression analysis. But we also include age in the back-calculation, since we consider that fish length estimates based on the otolith may depend on their age.

Regression is used to back-calculate fish length.

The regression analysis was made using otolith length (LOTO) and fish length (LFISH) for the 4785 otoliths sampled. Preliminary visual inspection of the data reveals various growth phases or "stages" defined by different straight lines. Regression was next performed on the data corresponding to each of these growth phases.

The first-two phases of lower growth are considered first. The first regression analysis, either with all data pooled, or separated into two groups, shows that two different lines can be defined. In this case, the systematic change of the inflexion is optimized by using Fisher's F. The inflexion point obtained in this way was used as a lower limit for the next analysis, and the process continued with all possible groupings of the data.

In another group of regression analyses, the distance to the outer border calculated from equation 1 was related to otolith length for each age. In this way we obtained a regression line for each annual ring (Table III). Then, using the measurements of the annual rings (ANi) as the independent variable, we can obtain the expected otolith length for each age.

To avoid errors due to morphological anomalies of the otoliths, or to sections which do not properly intersect the nucleus, a correction factor was calculated by dividing the actual otolith length by the otolith length estimated at the time of capture. This correction factor was multiplied by the otolith length estimated for each annual ring.

Finally, for the otolith lengths calculated in this way for the fitted regression line of LOTO-LFISH, we obtain the back-calculated fish lengths for each annual rings.

Estimated fish lengths were grouped by cohorts to analyse growth, and the mean values by age for each cohort subjected to ANOVA.

The normalized differences between the actual mean lengths at age and those estimated for each cohort were treated in the same way.

Comparison of the estimated mean lengths at age with those obtained by other techniques may provide a way of validating age in addition to the back-calculation method used here. To test this, we used the estimated mean lengths of Gandaras and Zamarro (1990) based on Canadian samples from Flemish Cap for 1981 to 1983. In addition, we analyse mean length frequency distributions by Bhattacharya's (1967) method for the Community cruises to Flemish Cap 1988-1991.

RESULTS.

The behaviour of the variables indicates that only fish weight and otolith weight require logarithmic transformation, since the logarithms of the standard deviations are distributed with respect to the logarithms of their means on a line with slope 1. The original data are used for the other variables.

The 4785 measured and weighed otoliths were used to calculate the regression between LOTO and LFISH (Table II). In this model, the lines define points which characterize corresponding changes in length at 23 and 46 cm. These points may be related to the change from pelagic to benthic life, partial recruitment of the juveniles which takes place at 2 years, and the onset of sexual maturity at 4-5 years.

With the corresponding data at each age LFISH/LOTO was regressed on WOTO (natural logarithm of otolith weight). The regression lines by age are shown in fig. 2, which shows that for equal values of LFISH/LOTO, otolith weight is higher in older fish. Also, the weight differences between individuals with higher and lower growth but of the same age diminish with age, which may result from compensatory growth. It should be mentioned that the regression obtained for age 1 has a much lower slope than expected (fig 2 and 3). This is probably due to the fact that age 1 fish are not completely recruit to the fishery, so that it is mainly the larger individuals which are caught.

The plot of successive slopes of the LFISH/LOTO-WOTO regressions by age is shown in fig. 3, which reveals a sudden change in slope at 5 years of age. This change may reflect physiological modifications. The age of first sexual maturity (50%) estimated at 5 years (Kuzmin 1990) may be the reason for this change.

Fig. 5 shows the general growth curve for all cohorts, as well as that based on back-calculation. The fact that growth is practically linear to the age of 8 stands out, after which the slope decreases markedly.

The high values estimated for age 1 which lie above the adjusted growth curve should be emphasized. We think this is mainly due to the fact that age 1 fish are not fully recruited (see fig 2 and 3). Thus the entry parameters for back-calculation of these individuals are for faster growing fish, and produce over-estimates of the back-calculations for this age.

Fig. 5 also shows the mean length of 0-group fish, which is slightly higher than expected, and may be due to gear selection.

The back-calculated values for each annual ring and cohort using ANOVA (table IV) were used to compare growth rates between years classes. We see that there are no significant differences except for ages 1, 2, and 3. We think this is due to the Lee (1912) phenomenon, which is revealed more clearly in the back-calculated lengths of the youngest fish.

To test this, we made the same analysis with the back-calculated lenghts grouped by age of individuals sampled. The ANOVA only identifies significant differences in the values estimated for the first three annual rings (Table V), but there seems to be a general tendency for back-calculated values to decrease as age increases as in Lee's phenomenon.

Thus the oldest cohorts studied give rise to lower back-calculated values than the more recent cohorts, which are comprised of younger fish in which Lee's phenomenon is not so apparent.

Fig. 4 shows the normalized difference between fish length and back- calculated fish length for each age grouped by cohorts, and shows that the 1985 and 1986 cohorts grew more slowly than the others.

Since there are no significant differences between length estimates based on otoliths and mean otoliths lengths, we think that the growth differences observed between cohorts are due to changes in the relation between fish length and otolith length.

In other works (P-Gandaras and Casas, in Preparation) following the criterion of Rätz (1990), the annual rings are classified in three categories (A, B, and C) as follows: well marked rings, absence of false rings and clearly visible hyaline zones (type A); weakly marked thin rings, often accompanied by false rings (type B); complex rings with complex structure, difficult to classify (type C).

It was found that the frequency of each type of ring is related to the occurrence of cold years in the Flemish Cap area. Thus cohorts which originated in abnormally cold years (1985, 1986) tend to have a higher proportion of type A rings at each age within each cohort, and less growth.

Perez-Gandaras and Zamarro (1990) also found a relation for Flemish Cap between cold years, lower growth and more abundant cohorts.

Thus despite the high correlation between otolith lenght and fish length , there is evidence of an allometric relation between otolith growth and fish growth, produced particularly during suboptimal conditions (Mugiya et al 1990). Mosegaard et al (1988) examined the effects of temperature, length and weight on the growth rate of otoliths of Artic char (<u>Salvelinus alpinus</u>). Amongst other results, they stated: (pp 1520) "The response of otolith growth rate to increasing temperature is totally different from the optimum curve of somatic growth rate, such that otolith growth rate continues to increase above temperatures of maximum somatic growth rate.".

No significant differences were found in growth between males and females , as shown in table VI. But in females, the typical deviation increases throughout life, in contrast to males where it seems to reach a maximum at 5 or 6 years old.

This may be due to reading errors as the females display spawning rings which can make interpretation difficult. Nevertheless Rollefsen (1933) described these spawning rings in Norwegian Cod as comparatively wide, more intensely hyaline, and following opaque zones which are narrower than expected. If these features are found in the otoliths of the Flemish Cap stock, then they should make them easier to read so that the errors could not be explained in this way.

Another possibility is based on so-called reproductive failure (Walsh et al *1986*). This phenomenon may affect female cod from Flemish Cap, which although mature do not spawn *every* year. This aspect of the reproductive dynamics of Flemish Cap cod is still not clear, and should be tackled for the stock studied here.

Fig. 6 shows the growth curves for the different cohorts. As well as the mean values by age from back-calculation, the mean lengths at capture are also included, from Canadian cruises on Flemish Cap in 1981-1983 analyzed by P-Gandaras and Zamarro (1990), as are also the modal values obtained by Bhattacharya from the Community cruises in 1988-1991. All these points fit the growth curves for each cohort well, validating the back-calculations of this study.

CONCLUSIONS

The high correlation index between fish length and otolith length renders it a suitable tool for the study of growth in Flemish Cap cod.

The inflexions in the LOTO-LFISH regression identify important physiological changes in the life of cod, associated with the change from pelagic to demersal life in the early years of life, and with the onset of sexual maturity.

For individuals of the same age, we find distinct LFISH/LOTO relationship which characterize different growth rates.

We also find that the otoliths of the oldest fish are heavier for the same LFISH/LOTO relationship.

The growth of Flemish Cap cod is practically linear until the age of 8 years, and then declines markedly.

The mean lengths at age of the different cohorts studied here obtained by back-calculation do not reflect the real differences in growth between cohorts. These differences seem to be linked to environmental conditions such as water temperature and year class abundance.

In adition to the morphometry of the otoliths and their rings, the study of ring types allows us to better understand the relations between the growth of fish and otoliths, which apparently vary with external conditions , and are the causes of growth differences between cohorts.

Finally, the comparison of mean lengths by age and cohort back-calculated with values obtained by other methods provides a useful way to validate our results.

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TABLE I.- Otolith numbers by age for the cohorts 1980-1990.

	COHORTS										
AGE	1980	1981	1982	1983	1984	1985	1986	1987	1988	1990	TOTAL
0										15	15
1							10	20	117		147
2						50	137	100	161		448
3					135	139	206	169	201		850
4				142	171	190	199	152			854
5			154	110	198	212	201				875
6		190	46	172	189	192					789
7	187	64	95	137	92						575
8	21	74	54	43							192
9	16	26	4								46
10	9										9
TOTAL	233	354	353	604	785	783	753	537	573	15	4800

TABLE II.- Linear Regression by groups. (LOTO) otolith length, (LFISH) fish length.

SMALL (<8.2)	LFISH = 2.5347 LOTO - 0.4382	R = 1.00
MEDIUM - SIZED (8.2 - 12.7)	LFISH = 4.5029 LOTO - 16.96141	R = 1.00
LARGE (12.8 - 19.7)	LFISH = 7.1915 LOTO - 51.24034	R = 1.00
LARGEST (> 19.7)	LFISH = 5.1429 LOTO - 10.29397	R = 0.98

TABLE III.- GM Regression (ANi) annual rings, (LOTO) otolith length.

AN1	LOTO = 11.84 AN1 + 0.62	R = 0.82
AN2	LOTO = 12.03 AN2 + 0.47	R = 0.94
AN3	LOTO = 11.97 AN3 + 0.84	R = 0.83
AN4	LOTO = 9.22 AN4 + 3.71	R = 0.81
AN5	LOTO = 10.08 AN5 + 2.54	R = 0.73
AN6	LOTO = 10.74 AN6 + 2.90	R = 0.65
AN7	LOTO = 8.96 AN7 + 5.62	R = 0.72
AN8	LOTO = 10.23 AN8 + 4.30	R = 0.74
AN9	LOTO = 9.94 AN9 + 4.92	R = 0.80
AN10	LOTO = 10.19 AN10+4.57	R = 0.73

TABLE IV.- Means of body lengths (cm) backcalculated by year class.

YEAR CLASS		ANNUAL RINGS								
	Nº	1	2	3	4	5	6	7	8	9
1980	51	15.49	22.59	31.76	41.70	54.49	66.56	76.82	86.34	94.25
1981	91	16.10	23.49	34.19	44.26	56.80	67.83	78.28	87.76	93.86
1982	83	16.41	23.71	33.58	43.59	56.67	67.36	77.18	90.00	91.31
1983	115	15.90	25.01	34.45	42.91	55.56	68.17	74.12	86.6	
1984	15	16.09	24.09	34.87	43.99	58.10	69.64	78.95		
1985	97	16.28	23.69	33.54	43.73	57.32	66.56			
1986	101	16.54	24.65	35.88	44.66	53.41				
1987	34	16.23	23.61	33.41	47.71					
Mean	677	16.15	24.02	34.26	43.61	56.43	67.32	76.90	87.32	93.13
F*		2.12	2.96	4.2	1.89	1.47	1.10	1.90	1.03	0.56
S**		S	S	S	NS	NS	NS	NS	NS	NS

* F-ratio found in one-way ANOVA between/within YEAR CLASS.
** S = Significant at P lt 0.05 level; NS = Not significant.

TABLE V.- Means of body lengths (cm) backcalculated by age group.

AGE GROUP		ANNUAL RINGS								
	Nº	1	2	3	4	5	6	7	8	9
1	23	15.81								
2	45	15.79	22.43							
3	79	16.58	24.87	35.13						
4	100	16.47	25.81	35.14	43.98					
5	121	16.35	24.11	34.36	44.03	56.81				
6	132	16.03	23.71	34.32	44.35	57.91	68.21			
7	86	15.94	23.44	33.14	42.46	55.03	66.62	76.29		
8	59	16.00	22.73	33.10	42.71	55.58	67.02	77.79	87.36	
9	46	15.63	22.79	32.67	42.11	54.55	66.21	76.86	87.35	92.82
10	20	15.13	21.78	31.06	40.52	52.61	63.81	74.69	84.65	91.44
Mean	713	16.12	23.94	34.15	43.38	56.21	67.03	76.61	86.75	92.19
F*		2.26	2.96	4.20	1.89	1.47	0.99	1.12	0.98	0.17
S**		S	S	S	NS	NS	NS	NS	NS	NS

* F-ratio found in one-way ANOVA between/within AGE GROUPS.
** S = Significant at P lt 0.05 level; NS = Not significant.

TABLE VI.- Means of body lengths (cm) back-calculated by sex.

ANNUAL RINGS	MALE	Nº	STANDAR DEVIATION	FEMALE	Nº	STANDAR DEVIATION	F*	S**
1	16.28	354	1.83	16.13	362	1.98	0.14	NS
2	23.82	344	3.58	24.01	349	3.53	0.49	NS
3	34.00	319	4.61	34.20	327	4.75	0.28	NS
4	43.56	279	5.67	43.29	288	5.60	0.31	NS
5	56.27	224	7.55	55.92	244	7.76	0.01	NS
6	66.93	163	7.93	66.76	182	8.92	0.02	NS
7	76.66	103	7.18	76.09	113	8.77	0.01	NS
8	86.70	63	7.11	87.26	65	9.56	0.20	NS
9	92.55	29	7.14	90.70	40	9.57	0.11	NS
10	97.96	5	2.78	92.38	18	11.15	0.72	NS

* F-ratio found in one-way ANOVA between/within sex.
** S = Significant at P lt 0.05 level; NS = Not significant.

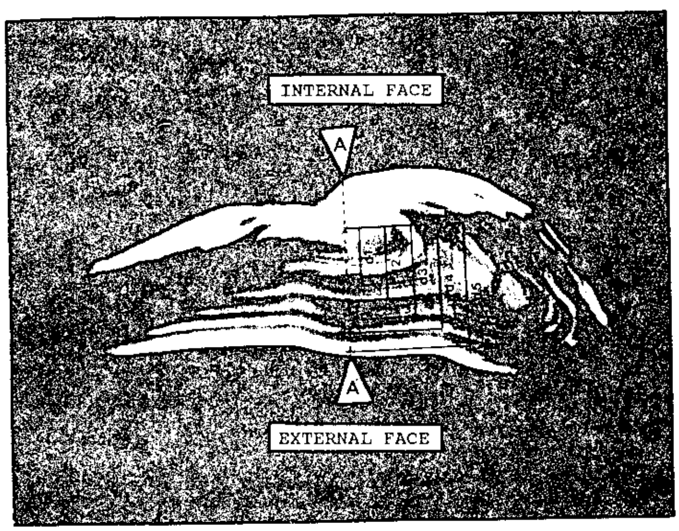


Fig 1.- Cod otolith section with the mesures taken for the Back-calculation.

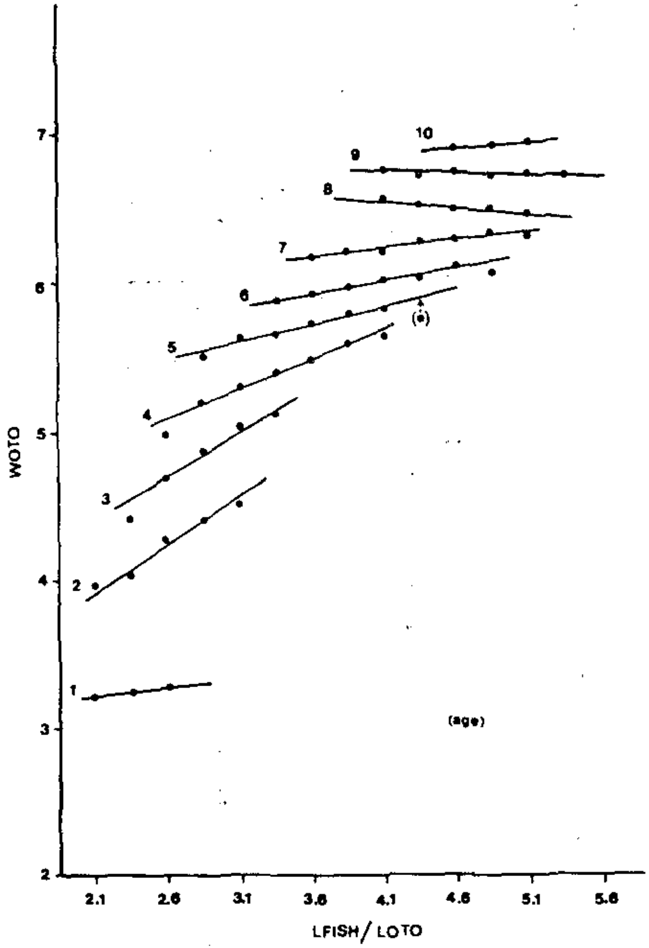


Fig 2.- Linear regression (LFISH/LOTO - WOTO) by cod age.

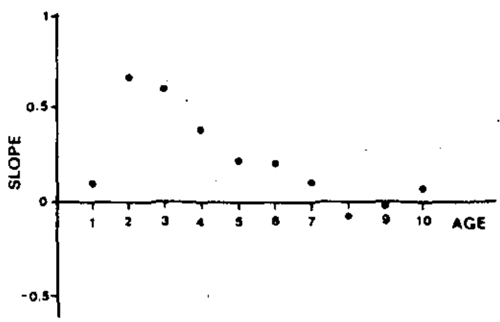


Fig 3.- Slopes of the linear regression (LFISH/LOTO - WOTO) by cod age.

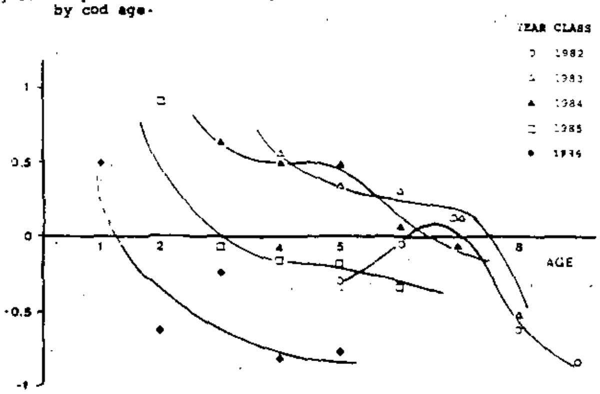
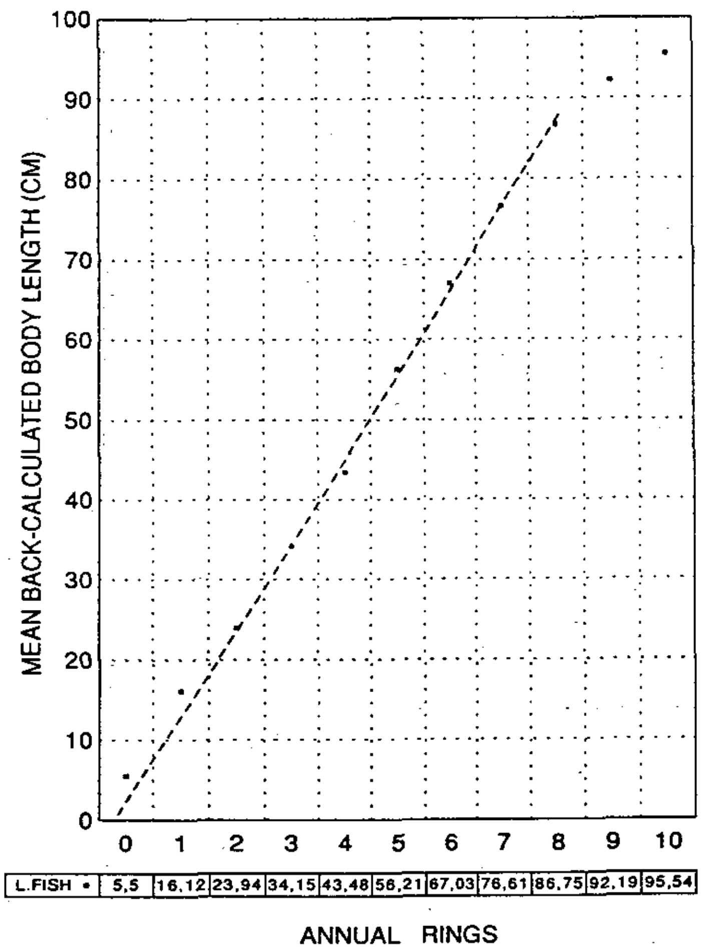


Fig 4.- Fish length estimated Fish length difference, normalized by age.



L.FISH •	5,5	16,12	23,94	34,15	43,48	56,21	67,03	76,61	86,75	92,19	95,54

Fig 5.- Back-calculated fish length.

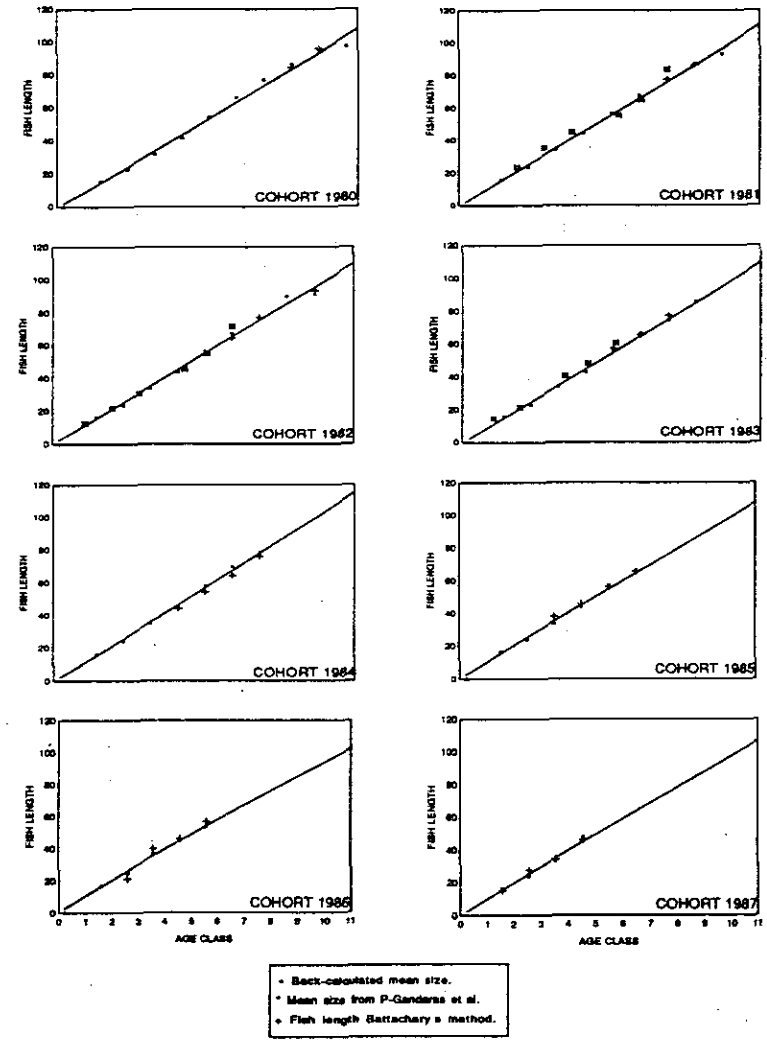


Fig 6.- LFISH by age class.